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# THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA. XIV. *LEWISUCHUS ADMIXTUS*, GEN. ET SP. NOV., A FURTHER THECODONT FROM THE CHAÑARES BEDS

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Abstract. Incomplete remains of a new thecodont from the Chañares Formation, *Lewisuchus admixtus*, are described and figured. Incomplete skull remains indicate that the posterior border of the lateral temporal opening was nearly vertical; the basal articulation with the palate was freely movable. A maxilla indicates elongation of the snout. Much of the presacral column is present; the cervical vertebrae are somewhat elongate, the ribs unspecialized. Scapulocoracoids are preserved, but no pelvic material; limb material is incomplete and disarticulated; femur and tibia are slender and of approximately equal length; the pes is long and slender. A single row of thin dorsal scales is present. *Lewisuchus* is a relatively primitive pseudosuchian that may be related to coelurosaur ancestry.

## INTRODUCTION

After much preparation and a general survey of the Chañares collection, it became apparent that six thecodonts of various sorts were present in the material; these have been described in previous papers in this series. Recently, however, Mr. Arnold Lewis, in preparing a concretion containing a mixed assortment of reptilian remains, discovered that in addition to parts of a gomphodont skeleton and miscellaneous materials of small thecodonts, there was present a considerable fraction of a skeleton and skull of a thecodont of relatively good size which was obviously new, and is described below.

I am indebted to the National Science Foundation grant GB-2454 for aid in the collecting of the specimen and grant GB-22658 for preparation and publication.

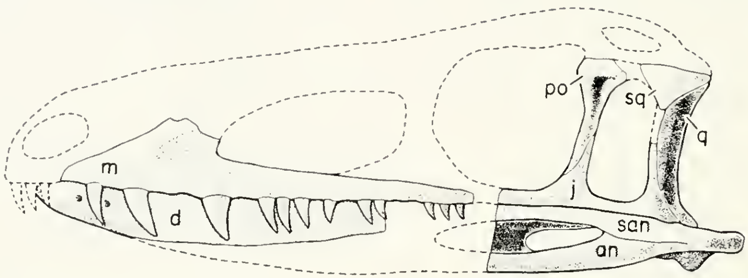



Figure 1. Lateral view of the skull, restored. *an,* angular; *d,* dentary; *j,* jugal; *m,* maxilla; *po,* postorbital; *q,* quadrate; *san,* surangular; *sq,* squamosal. The jugal-quadratojugal suture is obscure. × 2/3.

## *Lewisuchus admixtus,* gen. et sp. nov.

*Holotype.* Museo de La Plata 1964-XI-14-14, consisting of much of the presacral column, part of the skull and jaws, scapulororacoids and some limb material, contained in a concretion including also remains of a gomphodont and smaller thecodonts. The specimen was collected from the Chañares Formation of La Rioja Province, Argentina, about 4 km north of the mouth of the Chañares River.

The generic name is in honor of Chief Preparator Arnold D. Lewis, who discovered the remains during preparation of the nodule containing them. The specific name refers to the mixture of materials in the nodule.

## DESCRIPTION

*Skull and jaws* (Figs. 1–5). In one portion of the nodule were found the "cheek" region of the skull in articulation with the back end of the mandible, and close by, the occipital plate and basicranium, as well as a limited amount of other skull material. Separately were found an incomplete maxilla with dentition, an appropriate dentary, and a small segment of another maxilla and dentary.

Of the skull remains, the region of the left lateral temporal opening is well preserved (Fig. 1). The fenestra is subquadrate in outline, relatively narrow anteroposteriorly, the posterior margin descending vertically to the region of the jaw articulation. The jugal forms most of the straight lower margin of the skull in this area, the portion preserved running back from the area

below the orbit to a contact with the quadratojugal, and including a triangular process ascending between orbit and lateral temporal opening to a diagonal articulation with the postorbital. The latter bone extends down nearly to the posteroventral angle of the orbit, narrowing distally; this ventral portion of the bone has a vertical groove at mid-width. At the level of the top of the lateral fenestra the postorbital is thickened, with a pronounced transverse ridge on its outer surface. The bone is broken off shortly above this point.

The quadratojugal completes posteriorly the ventrolateral skull margin. Posteriorly, adjacent to the quadrate, it expands in triangular fashion and sends a slender process, curving somewhat forward, up along the anterior margin of the quadrate. This process, as preserved, terminates about half-way up the posterior margin of the lateral fenestra.

The quadrate is nearly complete. Below, it presents a broad area for jaw articulation; this area, however, is not well preserved and the surface was perhaps cartilaginous in life. Its external ramus sweeps far upward behind the lateral fenestra, with a mildly convex anterior border, and with a concave cross section. At the posterior margin of this ramus there is, as in thecodonts generally, a sharp ridge, internal to which is the ramus articulating with the pterygoid, little developed dorsally but of considerable extent further ventrally. Lying above the head of the quadrate is a triangular piece of bone, quite surely broken off dorsally, with its apex directed downward along the anterior edge of the quadrate, its posterior margin following the curved upper edge of the quadrate. Its curved anterior margin apparently formed the posterodorsal angle of the lateral fenestra. This is surely a fragment of the squamosal. It is probable that in life squamosal and quadratojugal were in contact along the anterior margin of the quadrate. Above the preserved portions of the postorbital and squamosal are several bone fragments of indeterminate nature which may have pertained to the missing skull roof.

Internal to the temporal area described above, but not articulated with it, is a nearly complete braincase (Figs. 2–4) mostly in a good state of preservation. No sutures are apparent. The occipital plate is complete. Above is a broad supraoccipital area, with a median vertical ridge dorsally. On either side the upper margins curve forward into the otic region of the braincase; below this, on either side, paroccipital processes, broadened at their tips, run outward and somewhat downward and posteriorly.

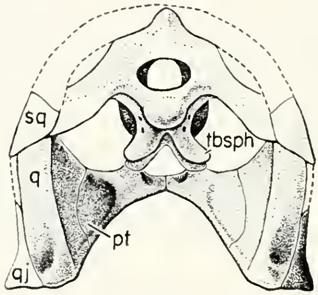



Figure 2. Posterior view of the skull; roof restored. *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal; *tbsph*, basisphenoidal tubera. × 1.

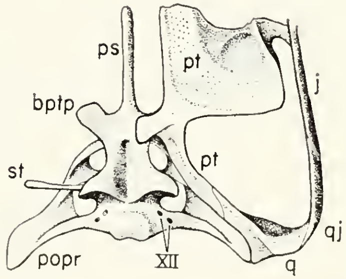



Figure 3. Ventral view of posterior part of skull; quadrate and dermal bones shown on right side of figure; ventral view of braincase on left. *bptp*, basipterygoid process of basisphenoid; *j*, jugal; *popr*, paroccipital process; *ps*, cultriform process of parasphenoid; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *st*, stapes; *XII*, openings for hypoglossal nerve. × 1.

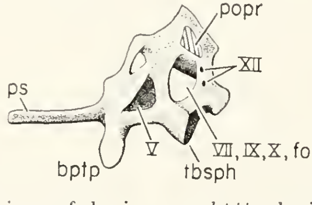



Figure 4. Lateral view of braincase. *bptp*, basipterygoid process; *fo*, foramen ovalis; *popr*, paroccipital process, cut off at base; *ps*, cultriform process of parasphenoid; *tbsph*, basisphenoidal tubera. Roman numerals indicate presumed region of nerve exits. × 1.

Below the large foramen magnum is the occipital condyle. Its surface is broad and somewhat subdivided posteriorly, and faces as much ventrally as posteriorly, suggesting a head posture appropriate to a possible bipedal pose. The basicranial region is well preserved. Just anterior to the condyle are highly developed basisphenoidal tubera. Broad posteriorly, they diminish in size anteriorly as they converge, with a deep longitudinal median groove between them. Anterior to the region of the bases of the tubera are highly developed basipterygoid processes, which extend strongly downward, outward, and somewhat anteriorly. It is obvious that at their curved articular termini there was free movement between the processes and the pterygoids. Extending forward between the base of the basipterygoid processes is the slender cultriform process of the parasphenoid, incomplete anteriorly.

The upper margins of the braincase stop at a point where presumably the roof of the brain cavity was continued by the dermal roofing bones. Laterally (Fig. 4), the upper margins curve forward on either side. The upper part of the lateral braincase walls slants medially; below this, a prominent if rounded ridge runs forward from the anterior surface of the paroccipital process, separating from the upper part of the wall a lateral surface which lies in a vertical plane and ventrally turns somewhat medially.

Three bars or "struts" constitute the lateral braincase wall connecting the upper portion of the braincase with the basicranial region. The most posterior, adjacent to the foramen magnum, is formed by the exoccipital, presumably reinforced anteriorly by opisthotic ossification. Two foramina are present in this strut. At least one was obviously occupied by nerve XII; possibly the other served for passage of the vagus nerve, but the opening is small and I tend to believe that this was a second hypoglossal foramen, and that the vagus emerged anterior to this strut.

Between the posterior and middle struts there is a large unossified area in the side wall of the otic region; presumably in this area lay the exits of nerve VII, the vagus foramen and the fenestra ovalis. The upper portion of the interval between posterior and middle struts is ossified, the ossification lying deep to the struts concerned. The middle strut is presumably formed by a prootic ossification, with nerve V emerging anteriorly beneath it. The most anterior strut, presumably a laterosphenoid ossification, descends to meet the basisphenoid at the base of

the basipterygoid process. Dorsally the presumed laterosphenoid bifurcates, leaving an opening (? a fenestra epioptica) between its branches and the dorsal taenia marginalis. No more anterior ossification is preserved in the braincase. The dorsal surface of the cultriform process is grooved, presumably for reception of a cartilaginous sphenethmoidal braincase segment.

Much of the left pterygoid is preserved, although it is somewhat displaced. The quadrate ramus is present. Its ventral border is strongly ridged, continuing a ridge present more posteriorly on the quadrate. Anteriorly this ridge curves upward, separating a thinner posterior portion of the ramus from a thicker anterior area; presumably this marks the boundary of the tympanic cavity. The area for articulation with the basipterygoid process is a recess on the medial border of the bone at the junction of quadrate and palatal rami. The posterior portion of the palatal ramus is preserved: there is no evidence of palatal teeth. A well-developed lateral flange appears to have extended directly laterally, with a slight ventral curvature distally. A ridged medial border of the ramus is preserved for a distance. From the tip of the lateral flange the lateral, ridged, margin of the palatal plate curves forward and somewhat medially and dorsally; for the short distance preserved, the lateral border twists sharply outward and gains contact with the jugal. It is probable that this region pertains to an ectopterygoid, and there is some evidence of a line of suture between this element and the pterygoid.

On the right side a slender splint of bone, about 7 mm long, extends outward from the braincase region anterior to the paroccipital process. This is reasonably identified as a stapes.

No more anterior portions of the skull are present in articulation with, or near, the posterior skull elements so far described. Probably pertaining to this skull are tooth-bearing elements that are certainly thecodont in nature and of appropriate size. A tooth-bearing strip of bone, 73 mm in length, is surely an incomplete right maxilla (Fig. 1). The teeth are incompletely preserved, but some 18 teeth or alveoli can be counted. A maximum size appears to be developed not far from the anterior end, posterior to which there is a gradual diminution in tooth size. Externally, near the anterior end there is a curved ridge that presumably marks the border of the depression containing the antorbital fenestra. Part of the upper margin of the maxilla appears to be a finished surface bounding the fenestra. The internal surface of the bone is considerably swollen in the area in which the bases of the larger teeth were contained; above this

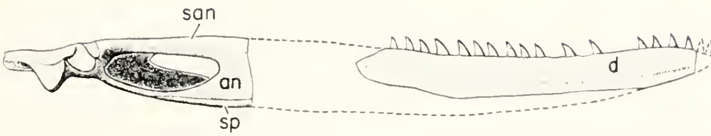



Figure 5. Inner view of lower jaw, restored. *an*, angular; *d*, dentary; *san*, surangular; *sp*, splenial. × 2/3.

is a thin area that is obviously part of the maxillary extension upward anterior to the antorbital fenestra. It may be noted that the tooth row is essentially straight, without the ventral convexity noticeable in carnosaurs and even in ornithosuchids.

A fragment that pertains to a left maxilla shows a series of teeth clearly decreasing in size posteriorly. As in thecodonts generally, the teeth are somewhat compressed mediolaterally, conical, sharp-pointed, and recurved posteriorly toward their tips.

The posterior portion of the left mandible is present in essentially natural relations with the cheek elements and quadrate (Figs. 1, 5). The anterior end of the preserved portion lies in the region of the external mandibular foramen, showing above this opening the surangular and, below, the angular and posterior end of the splenial. Internally the jaw portion preserved shows the suture outline of the mandibular fossa. It is probable that in life the outer surface of the ramus was tilted strongly medially, but, even so, it would appear that the fossa faced as much medially as dorsally. Above the fossa the jaw, as preserved, appears to show a broad horizontal shelf along the course of the surangular. The articular surface of the mandible is large, broadened lateromedially, and divided into a smaller anterior and larger posterior portion; the articulation is so oriented that the inner margin is somewhat more anteriorly placed. There is a well-developed retroarticular process and, in addition, a strong flange directed ventromedially behind the articular area.

Presumably belonging to this specimen is an isolated tooth-bearing element, obviously a dentary, 62 mm in length, which bears about 20 teeth or alveoli (Figs. 1, 5). As frequently in thecodont jaws, there is no great regional difference in tooth size along the series. It is probable, from the contours of the bone, that little is absent anteriorly. Two small foramina for blood vessels are present close to the front end; internally a longitudinal meckelian groove is present, above which the bone is thickened for tooth roots.

In Figure 1 I have attempted to restore the skull in lateral view. Because of the relative length of the maxilla, it is obvious that the "snout" was much longer, relatively, than in many thecodonts.

*Axial skeleton.* Not connected with the cranial remains first described, but reasonably associated because of thecodont nature and proper size, is a series of 17 articulated vertebrae, beginning with the axis; part of this series is shown in Figure 6. Anterior to the axis are imperfect remains that appear to represent the atlas centrum and axis intercentrum (no intercentra are present more posteriorly). The axis is well developed, with a relatively low but long neural spine, with a curved upper margin. The cervical vertebrae are elongate as compared with the rest of the column; the axis centrum is 14 mm in length, and the more posterior cervicals are approximately similar, compared to an average of 11 mm in dorsal members of the series. Neural spines are not well preserved in the cervical region (the axis apart). In vertebra 8 the spine is low, extending but 9 mm above the level of the zygapophyses. The back border of the spine is essentially vertical, but the anterior border slants strongly forward dorsally, so that, from a width of 5 mm across the base, the dorsal margin is 10 mm in extent. There is no thickening of the dorsal margin for armor support (such as is seen in *Gracilisuchus*). In the dorsal region the spine bases are stouter, but the anterior slant of the anterior margin persists. There are some poorly preserved traces of scutes above the cervical vertebrae, apparently thin and probably in a single row.

As preserved, the cervical centra appear to be thin, compressed from side to side except for prominent vertical ridges at either end. Even here, however, there appears to be no sharp ventral longitudinal ridge, and as we proceed posteriorly the centra become thicker and but gently rounded ventrally. In the cervical region the sides of the centra show a longitudinal depression; farther back, with major development of the transverse processes, this depression is part of a more expanded excavation, bounded above by the roots of the transverse processes. The articular area for the rib capitulum lies, in the cervical region, at the base of the ridge forming the anterior margin of the centrum; it is, however, little marked in the column as preserved. Presumably this articular area ascended toward or to the arch in the posterior part of the series but there is little evidence preserved in the specimen. In the column as preserved the diapophysis is not

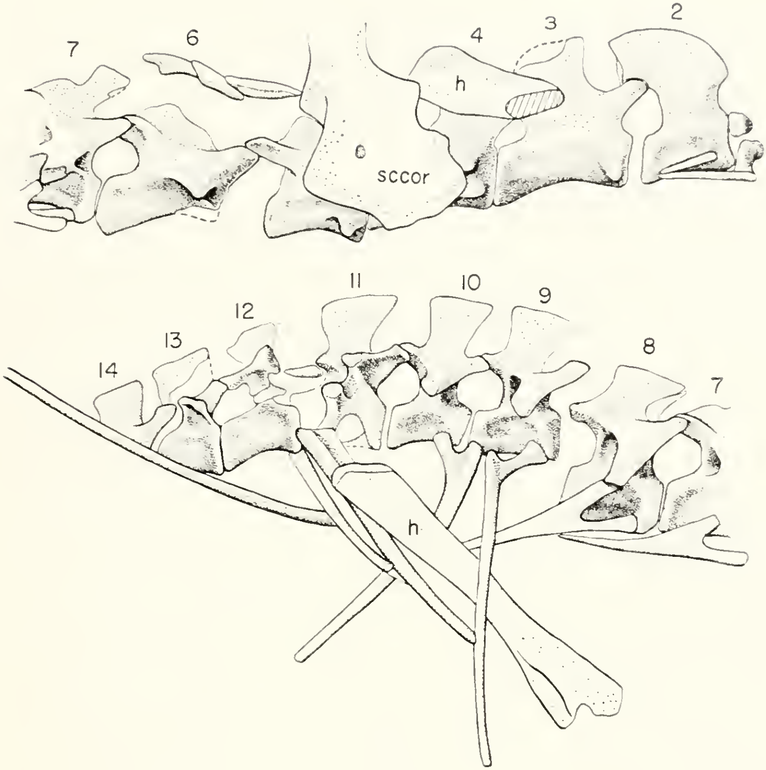



Figure 6. Right lateral view of cervical and anterior dorsal vertebrae and ribs. *h*, head of right humerus and incomplete left humerus; *sccor*, inner view of right scapulocoracoid. × 1.

prominently developed in the cervical vertebrae; in the dorsal region, however, the transverse processes become prominent, extending strongly outward and somewhat downward and backward. The process is supported ventrally by ridges extending upward to its base from both anterior and posterior margins of the centrum; above, a stout ridge connects the base of the process with the anterior zygapophysis, and a less developed ridge extends to the region of the postzygapophysis.

Close to the posterior end of the articulated series are three further vertebrae of appropriate size for *Lewisuchus*. Details are not well preserved, but presumably these vertebrae were from

the "lumbar" or sacral region. Several further isolated vertebrae are present in the concretion, not well preserved except for one which is clearly a posterior dorsal.

Ribs are in general incompletely preserved (Fig. 6). Close to the base of the axis centrum is a short rodlike structure, expanded at one end, which is presumably an incomplete axial rib; adjacent to it is a slender rod, 14 mm long, which may be an atlantal rib. There are no ribs preserved associated with cervicals 3–6; ribs are present, although incomplete, with vertebrae 7–10. All are markedly two-headed; there is no evidence of the development of accessory processes of the rib heads described in a number of other thecodonts. The preserved portions of these ribs, measured from the tubercula, are 20, 15, 45, and 37 mm long. Although none of the four is complete, the first two appear to be slender and close to their termini where broken off; the last two are more stoutly built and seem surely to have been true dorsal ribs. A few further incomplete rib segments are present close to the articulated rib series. In another part of the nodule are several articulated dorsal ribs of a size appropriate for *Lewisuchus*; one has a length of about 80 mm. The curvature of these ribs suggests a deep but narrow trunk. Close to the three vertebrae mentioned above as possible lumbars or sacrals are two structures with triangular outlines and with a developed articular area at the narrow end; these may be sacral ribs.

*Appendicular elements.* Close to, and quite surely pertaining to the articulated vertebral series are two scapulocoracoids (Fig. 7), the left seen from the outer surface, the right from the inner side. Scapula and coracoid are well fused, with no apparent suture. The scapular blade is unusually tall and slender. Distally it expands somewhat; the distal margin is taller posteriorly, slanting downward toward the anterior margin. The lower part of the scapula expands both anteriorly and posteriorly, with a thickened acromial ridge anteriorly and a somewhat comparable posterior ridge buttressing the upper glenoid rim. The ventral margins of the coracoids are imperfectly preserved, but the bone seems to be primitive in structure, with no evidence of a crocodiloid posteroventral extension, and without evidence of any anterior "incision" in the plate.

There is no material interpretable as being a clavicle or interclavicle of this specimen. And nothing found in this concretion can be identified as pertaining to the pelvic girdle of *Lewisuchus.*

There is a considerable amount of limb material strewn through the concretion, but most appears referable to a gompho-

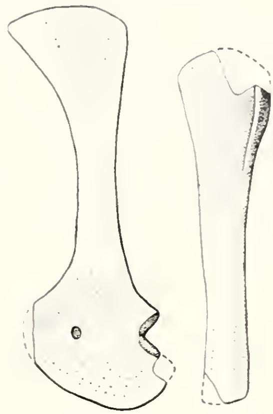


Figure 7. *Left,* left scapulocoracoid; *right,* incomplete left humerus in ventral view. × 1.

dont or to one or more thecodonts of smaller size. Only a small amount of material appears to be of a size and nature appropriate to *Lewisuchus.*

Close to the right scapulocoracoid is the head of a humerus obviously of slender build and a second imperfect humerus (Fig. 7); its head seems comparable to that just mentioned. The shaft is slender; the distal end is missing, but if extrapolated from the part present, on the analogy of *Hesperosuchus* (Colbert, 1952, fig. 22), the length in life must have been on the order of 70 to 75 mm. I find no elements that are interpretable as radius or ulna. A femur of appropriate size (Fig. 8) measures 105 mm in length. The bone is badly crushed proximally; it nevertheless shows a well-developed greater trochanter and an apparently spherical head turned in sharply from the shaft. The bone is slender, the shaft having a diameter of but 7 mm. Unfortunately the distal end is imperfect.

A slender tibia, represented mainly by an impression in the matrix, is 106 mm in length. Near the shoulder region (but also close to the vertebrae mentioned as perhaps being in the lumbosacral region) is a group of podial elements (Fig. 8B). Two slender bones, measuring 31 and 30 mm in length, are surely metapodials; semi-articulated with the second are three phalanges, the terminal one clawed. Near the first of the two metapodials is a relatively long phalanx, and beyond it a second series of three articulated phalanges, terminating in a clawed element.

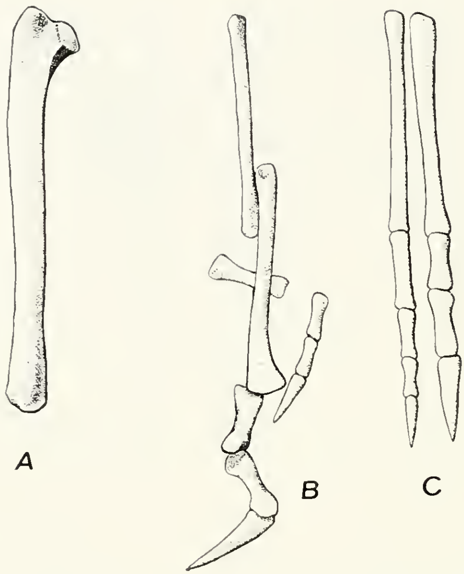



Figure 8. *A*, Right femur in dorsal view (incomplete distally); *B*, elements of second and third toes of right pes; *C*, the same, articulated. × 1.

It is most reasonable to interpret the two metapodials and the seemingly associated phalanges as toes II and III of the right pes. When articulated (Fig. 8C), it is obvious that digit II is stronger than III, and nearly as long, suggesting comparison with the proterochampsid type of foot (Romer, 1972a).

## DISCUSSION

Because of the inadequacy of the material, I have refrained from attempting a skeletal restoration of *Lewisuchus*. In default of good skull material, allocation of *Lewisuchus* to a definite position in the order Thecodontia is difficult. The modest trend toward strengthening of the inner toes immediately suggests comparison with *Chanaresuchus* (Romer, 1971; 1972a) and the proterochampsids, an assignment with which facial elongation is compatible. But strengthening of the inner toes is not confined to the proterochampsids, and the subquadrate configuration of the lateral temporal opening is sufficient to debar *Lewisuchus* from the Proterochampsidae, and indeed, from the suborder Proterosuchia, in which the lateral opening is relatively long

with the quadrate slanting backward ventrally. *Lewisuchus* is thus probably assignable to the Pseudosuchia.

*Lewisuchus* retains certain primitive features, such as the free basal articulation between palate and braincase, and the nearly straight back margin of the lateral temporal fenestra, which lacks the V-shape here found in many advanced forms. On the other hand, the long slender tibia, about equal to the femur in length, and the long metapodials, suggest a strong advance towards a truly bipedal gait.

*Lewisuchus* does not appear to be closely comparable to other described pseudosuchians. It differs in many obvious features from the ornithosuchids (cf. Romer, 1972b). It is possibly related to *Hesperosuchus* of Colbert (1952), but this form is poorly known and, furthermore, appears to differ in certain features, such as the incipient development of accessory rib flanges, absent in *Lewisuchus*. Elongation of cervical vertebrae suggests comparison with *Teleocrater*, an incompletely known form from the Manda beds, under description by Charig (1957). *Lewisuchus* may possibly be a form leading toward the coelurosaurs. Not improbably *Lewisuchus* may eventually merit being made the type of a family of its own. But for the time being it is perhaps best left as a pseudosuchian *incertae sedis*.

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